6-2005

The ecology and evolution of patience in two New World monkeys

Jeffrey R. Stevens
University of Nebraska-Lincoln, jstevens5@unl.edu

Elizabeth V. Hallinan
Harvard University, 5evh@queensu.ca

Marc D. Hauser
Harvard University

Published in *Biology Letters* 1:2 (June 22, 2005), pp. 223–226;
doi: 10.1098/rsbl.2004.0285 ; PMCID: PMC1626214

Submitted October 14, 2004; accepted November 8, 2004;
published online April 20, 2005.

The ecology and evolution of patience in two New World monkeys

Jeffrey R. Stevens, Elizabeth V. Hallinan, and Marc D. Hauser

Department of Psychology and Primate Cognitive Neuroscience Laboratory, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA

Corresponding author — J. R. Stevens

Abstract

Decision making often involves choosing between small, short-term rewards and large, long-term rewards. All animals, humans included, discount future rewards—the present value of delayed rewards is viewed as less than the value of immediate rewards. Despite its ubiquity, there exists considerable but unexplained variation between species in their capacity to wait for rewards—that is, to exert patience or self-control. Using two closely related primates—common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*)—we uncover a variable that may explain differences in how species discount future rewards. Both species faced a self-control paradigm in which individuals chose between taking an immediate small reward and waiting a variable amount of time for a large reward. Under these conditions, marmosets waited significantly longer for food than tamarins. This difference cannot be explained by life history, social behavior or brain size. It can, however, be explained by feeding ecology: marmosets rely on gum, a food product acquired by waiting for exudate to flow from trees, whereas tamarins feed on insects, a food product requiring impulsive action. Foraging ecology, therefore, may provide a selective pressure for the evolution of self-control.

Keywords: temporal discounting, impulsivity, rate maximization, tamarins, marmosets

1. Introduction

How individuals discount or devalue future rewards has intrigued economists, psychologists and behavioral ecologists under a number of different guises. Researchers studying temporal discounting often have subjects choose between small, immediate and large, delayed rewards to assess whether they can exhibit self-control by waiting for the delayed reward, or whether they discount the value of the delayed reward and select the immediate reward. Economists have examined discounting as a crucial factor in constructing models of how humans assign utility to rewards available over different time-scales (Frederick *et al*. 2002). Psychologists commonly use self-control paradigms to investigate the cognitive mechanisms associated with delayed gratification and impulsivity in humans and non-human animals (Logue 1988). Behavioral ecologists investigate rate maximization to elucidate the role of evolutionary pressures influencing animal foraging ecology (Kacelnik 2003). These three perspectives converge in their finding that the speed with which individuals devalue delayed rewards (the "discounting level") can vary tremendously between species, between individuals, across the lifetime of a single individual, and even in different contexts for the same individual. Why does this variation exist? Researchers suggest that some of this variation could result from differences in the rate of interruptions (Sozou 1998) or general cognitive ability (Tobin *et al*. 1996). Understanding the source of this variation could help elucidate the causes of impulsivity and self-control.

Here, we examine discounting behavior in two cooperatively breeding New World monkeys—common marmosets and cotton-top tamarins. These species have comparable body and brain size, behavior, mating systems and life history trajectories (Table 1). Given the similarities and relatively close phylogenetic relationship between these species, one might not expect substantial differences in cognitive abilities such as discounting. A closer look at their foraging ecology, however, reveals one factor that might favor different discounting functions: in general, marmosets are significantly more gummivorous when compared with tamarins (approximately 70% versus 14% of feeding time, respectively; Snowdon & Soini 1988; Stevenson & Rylands 1988), whereas tamarins are more insectivorous. Gummivory requires scratching tree bark and then waiting for the sap to flow, while insectivory favors immediate acquisition of an ephemeral food source.

2. Material and Methods

To evaluate the discounting behavior of both species, we used an adjusting-delay, self-control procedure (Mazur 1987). Captive-born subjects, with no foraging-relevant experience, chose between two tools, one containing a small, immediate reward and the other containing a large, delayed reward (figure 1). We presented each subject with a series of 15–32 experimental sessions composed of 10 choice trials. In each trial, a subject selected between two options, the "standard" option of two food pellets with no delay and the "adjusting" option of six food pellets with variable delay. Initially, there was no delay between pulling either tool and receiving access to the food. If the subject preferred the larger reward, we incremented the delay to the large reward by 1 s on the subsequent session. If the subject preferred the small reward, we decreased the delay to the large reward by 1 s. If the subject selected the two amounts equally often, the delay to the large reward remained the same. Using this method, we titrated the delay time to find each subject's indifference point—the point at which subjects equally valued the smaller, immediate reward and larger, delayed reward (see Supplementary Materials).

3. Results

On average, tamarins showed indifference between the amounts when the six pellets were delayed for a mean (± s.e.) of 7.9 ± 0.6 s, whereas marmosets waited 14.4 ± 1.5 s (Figure 2), a significantly longer delay ($F_{1,7}$ = 13.51, $p < 0.01$). The indifference points for individual tamarins ranged from 5.6 to 9.8 s, and for marmosets from 10.0 to 19.0 s; the most self-controlled tamarin waited less than the most impulsive marmoset. We next turn to an analysis of why such species differences may have evolved.

Table 1. Comparison of traits for tamarins and marmosets.

Trait	Cotton-top tamarins (*Saguinus oedipus*)	Common marmosets (*Callithrix jacchus*)
body weight[a]	380 g[b]	280 g[b]
brain weight[a]	10 g	7.6 g
brain/body weight ratio[a]	0.026	0.027
lifespan[c]	11.7 yrs	13.5 yrs
home range size[d]	7.8–10 ha	0.5–5 ha
habitat[d]	lower to mid-canopy of Colombian rainforest	lower to mid-canopy of Brazilian rainforest
group size[d]	2–13	3–13
mating system[d]	monogamy, occasional polyandry	monogamy
parental care[d]	bi-parental care	bi-parental care
cooperative breeding[d]	yes	yes
twinning[d]	common	common
diet[d]	insects > fruit > gum	gum > insects > fruit
percentage time feeding on gum[d]	14%[e]	70%

a. Stephan *et al.* (1981).

b. Note that these values are estimates from Stephan *et al.* (1981) to correlate with their measures of brain size. Weights for our subjects can be found in the Supplementary Material.

c. Ross (1991).

d. Snowdon & Soini (1988) and Stevenson & Rylands (1988).

e. No data available for *Saguinus oedipus*, therefore we used a measurement for closely related *Saguinus geoffreyi*.

Body condition (body weight/tibia length) did not significantly correlate with indifference points for either marmosets ($r^2 = 0.33$, $p = 0.31$) or tamarins ($r^2 = 0.01$, $p = 0.89$), excluding the influence of motivational state on choice behavior. Some researchers suggest that the level of discounting may decrease with the ratio of brain size to body weight (Tobin *et al*. 1996). This explanation cannot account for our differences in discounting, as the brain : body ratio of tamarins (0.026) is almost identical to that of marmosets (0.027; Stephan *et al*. 1981).

To quantitatively assess how the marmosets and tamarins devalue rewards over time, we tested whether the patterns of discounting fit predictions made by the rate maximization model of discounting. Rate maximization theory predicts that foragers optimize the gain in reward per unit time (Stephens & Krebs 1986); therefore, individuals should maximize the fitness value (V) of a choice $V = A/(t+h)$, where A is the reward amount, t is the delay to reward following choice and h is the time required to process/handle the reward. Note that this function describes only short-term gain, omitting the time between choices. Despite its intuitive appeal, psychologists and behavioral ecologists have demonstrated that animals tend to ignore the inter-choice interval, maximizing intake over the short-term rather than the long-term (Bateson & Kacelnik 1996; Stephens & Anderson 2001). Rate maximization predicts indifference between the small and large rewards in our design when intake rate of the standard option equals that of the adjusting option: $A_s/(t_s+h_s) = A_a/(t_a+h_a)$. Given the values from Table 2, we can estimate the predicted indifference point (t_a) if the subjects maximize intake rate. Because of differences in handling time between species, rate maximization predicts an indifference point of 8.6 s for tamarins and 6.6 s for marmosets (table 2). While the marmosets waited longer than expected by the rate maximization model ($t_8 = 4.5$, $p < 0.01$), the tamarins' mean indifference point did not differ from the rate maximization prediction ($t_{10} = -0.1$, $p = 0.91$). Thus, the tamarins appear to maximize their short-term intake rate, whereas the marmosets have a longer time horizon, resulting in more self-controlled choices.

4. Discussion

The striking difference in discounting behavior between tamarins and marmosets is surprising given their close phylogenetic relationship and comparable biology. The two species share similar mating systems, group sizes, cooperative behaviors and general ecology (Table 1). We suggest that a key difference between these species—their feeding ecology—may explain this difference.

Relative to other factors, ecological differences between species have been little explored as a selective pressure on discounting. As noted, one significant ecological difference between marmosets and tamarins is their diet. Although both species feed on fruit, marmosets specialize on plant exudates whereas tamarins focus more on insects (Coimbra-Filho & Mittermeier 1976; Snowdon & Soini 1988; Stevenson & Rylands 1988). Feeding on insects may require greater impulsivity to take advantage of ephemeral bouts of availability. Foraging on exudates has led to a number of specialized adaptations in marmosets such as modified teeth for gouging and modified digestive physiology (Coimbra-Filho & Mittermeier 1976; Harrison & Tardif 1994; Power & Oftedal 1996). Harrison & Tardif (1994) also contend that the concentrated nature of gum-exuding feeding sites may reduce gummivore home range sizes, possibly accounting for the differences between tamarins and marmosets. We contend that gummivory may have led to cognitive specializations as well. Because feeding on exudates requires waiting for gum and sap to ooze out of the plants, marmosets may have evolved the ability to value future rewards more than the insectivorous tamarins. Therefore, the self-control needed to feed on gums may have selected for a more general ability to delay gratification. The question remains: did selection increase impulsivity in tamarins, decrease it in

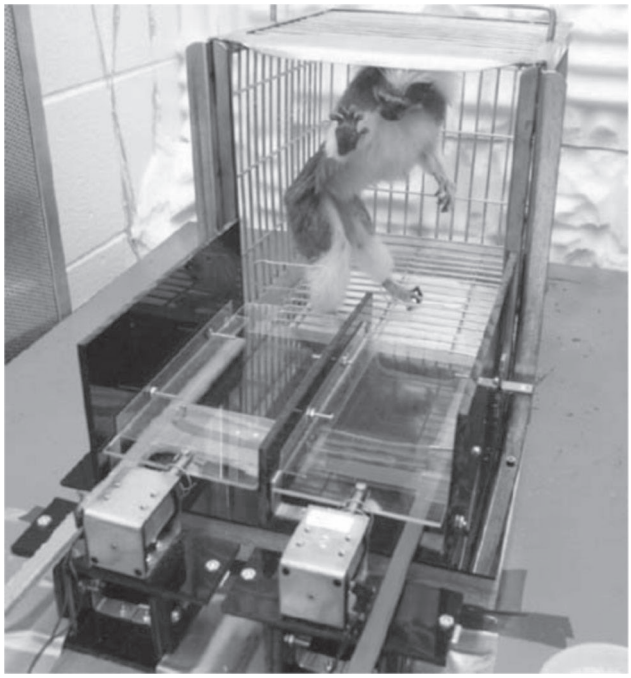

Figure 1. Experimental apparatus for discounting procedure. Both marmosets and tamarins experience the same choices: pulling one of two tools. One tool yielded two food pellets after no delay, and the other tool yielded six food pellets after a longer delay. Transparent Plexiglas covers prevented access to the pellets until the delay expired.

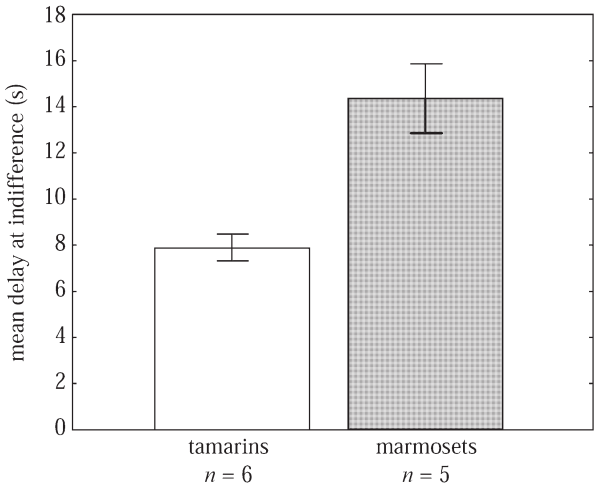

Figure 2. Species differences in discounting levels. Marmosets and tamarins differed in their indifference points with marmosets waiting almost twice as long for the six pellets than tamarins. The tamarin indifference point does not differ from that expected, but marmosets exhibit more self-control than predicted by short-term rate maximization. Error bars represent standard error of the mean indifference points.

marmosets, or both? Given our finding that tamarins' feeding rate maximizes but marmosets are more self-controlled than expected, it appears as though selection probably favored self-control in the marmosets.

The role of feeding ecology in cognition has been documented in other species. Species that cache food have better spatial memory (Balda & Kamil 1989) and larger

Table 2. Summary of amounts, delays and indifference points.

	cotton-top tamarins (*Saguinus oedipus*)	common marmosets (*Callithrix jacchus*)
standard amount (A_s)	2 pellets	2 pellets
adjusting amount (A_a)	6 pellets	6 pellets
standard delay (t_s)[a]	0.1 s	0.1 s
standard handling time (h_s)[a]	10.7 s	8.3 s
adjusted handling time (h_a)[a]	27.1 s	18.5 s
predicted indifference point (t_a)—rate maximization[a]	8.6 s	6.6 s
observed mean indifference point	7.9 s	14.4 s

a. See Supplementary Material for calculations of these estimates.

hippocampal volume (Basil *et al*. 1996) than closely related non-caching species. In addition, fruit-eating primates, such as spider monkeys, have larger brains than leaf-eating species such as howler monkeys, presumably to track spatial and temporal variation in fruit distribution (Milton 1981). The present study, however, provides the first indication that diet may influence animal discounting levels. If this model generalizes beyond the current findings, animals with long food processing times would exhibit more self-control than those with short processing times (but traveling time should not affect discounting). Therefore, we predict that species that must wait for food sources (e.g. gummivores, stalking predators) should have longer time horizons and lower discounting levels than species which immediately consume ephemeral food sources (e.g. frugivores, opportunistic predators); these ecological pressures may be so fundamental that even under captive conditions, innate species-specific differences are nonetheless maintained.

While highlighting differences in discounting levels between marmosets and tamarins in the context of foraging, our data do not necessarily imply a difference across all situations. In fact, selection may act on discounting levels in different contexts independently. For example, although tamarins and marmosets value food differently over time, they may value reproductive opportunities equally, given their similar mating systems. Yet, in more promiscuous systems in which each reproductive attempt is more valuable, individuals may act more impulsively in their mating decisions. Wilson & Daly (2004) provide data illustrating how discounting might interact with reproduction in humans by demonstrating that men discount monetary rewards more highly following the presentation of attractive female faces, but not unattractive faces. They conclude that the possibility of mating makes men more impulsive. Studies that correlate discounting levels across contexts are needed to determine the domain specificity of these cognitive adaptations.

One alternative explanation of our findings is that rather than having different discounting levels, tamarins and marmosets value the food differently—that is, perhaps marmosets value six pellets as more than three

times the value of two pellets and, therefore, will wait longer for them. While difficult to rule out, this alternative seems unlikely given that motivational measures which would temporarily influence value (such as body condition) did not correlate with individual indifference points. What remains are inherent differences in value functions between species, which are notoriously difficult to describe. Further work on varying quantities and qualities of food, as well as different methods of delaying access to food, is needed to disentangle the complex interaction between inherent value and temporal discounting.

Acknowledgments—We are grateful for funding from the National Research Service Award (NIH) to J.R.S., the Harvard College Research Program to E.V.H., and an NSF-ROLE grant to M.D.H. We thank Sarah Heilbronner, Diana Rodin and Victoria Wobber for assistance in conducting the experiments. We appreciate comments on earlier versions of the manuscript from Fiery Cushman, Alex Kacelnik, David Laibson, David Stephens and Margo Wilson, as well as two anonymous reviewers.

References

Balda, R. P. & Kamil, A. C. 1989 A comparative study of cache recovery of three corvid species. *Anim. Behav.* 38, 486–495.

Basil, J. A., Kamil, A. C., Balda, R. P. & Fite, K. V. 1996 Differences in hippocampal volume among food storing corvids. *Brain Behav. Evol.* 47, 156–164.

Bateson, M. & Kacelnik, A. 1996 Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav. Ecol.* 7, 341–352.

Coimbra-Filho, A. F. & Mittermeier, R. A. 1976 Exudate-eating and tree-gouging in marmosets. *Nature* 262, 630.

Frederick, S., Loewenstein, G., & O'Donoghue, T. 2002 Time discounting and time preference: A critical review. *J. Econ. Lit.* 40, 351–401.

Harrison, M. L. & Tardif, S. D. 1994 Social implications of gummivory in marmosets. *Am. J. Phys. Anthropol.* 95, 399–408.

Kacelnik, A. 2003 The evolution of patience. In *Time and decision: Economic and psychological perspectives on intertemporal choice* (ed. G. Loewenstein, D. Read, & R. Baumeister), pp. 115–138. New York: Russell Sage Foundation.

Logue, A. W. 1988 Research on self-control: An integrating framework. *Behav. Brain Sci.* 11, 665–709.

Mazur, J. E. 1987 An adjusting procedure for studying delayed reinforcement. In *Quantitative analyses of behavior: The effect of delay and of intervening events on reinforcement value,* vol. 5 (ed. M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin), pp. 55–73. Hillsdale, NJ: Lawrence Erlbaum Associates.

Milton, K. 1981 Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *Am. Anthropol.* 83, 534–548.

Power, M. L. & Oftedal, O. T. 1996 Differences among captive callitrichids in the digestive responses to dietary gum. *Am. J. Primatol.* 40, 131–144.

Ross, C. 1991 Life history patterns of New World monkeys. *Int. J. Primatol.* 12, 481–502.

Snowdon, C. T. & Soini, P. 1988 The tamarins, genus *Saguinus*. In *Ecology and behavior of neotropical primates* vol. 2 (ed. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho, & G. A. B. Fonseca), pp. 223–298. Washington, DC: World Wildlife Fund.

Sozou, P. D. 1998 On hyperbolic discounting and uncertain hazard rates. *Proc. R. Soc. B* 265, 2015–2020.

Stephan, H., Frahm, H. & Baron, G. 1981 New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* 35, 1–29.

Stephens, D. W. & Anderson, D. 2001 The adaptive value of preference for immediacy: When shortsighted rules have farsighted consequences. *Behav. Ecol.* 12, 330–339.

Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton University Press.

Stevenson, M. F. & Rylands, A. B. 1988 The marmosets, genus *Callithrix*. In *Ecology and behavior of neotropical primates,* vol. 2 (ed. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), pp. 131–222. Washington, DC: World Wildlife Fund.

Tobin, H., Logue, A. W., Chelonis, J. J. & Ackerman, K. T. 1996 Self-control in the monkey *Macaca fascicularis*. *Anim. Learn. Behav.* 24, 168–174.

Wilson, M. & Daly, M. 2004 Do pretty women inspire men to discount the future? *Proc. R. Soc. B* 271 (Suppl. 4), 177–179.

Supplementary Material follows.

Supporting Material

Material and Methods

Subjects

We used six adult cotton-top tamarins (three males and three females) and five adult common marmosets (three males and two females) as subjects in this experiment (See Table S.1 for more information). All subjects participated in other behavioural experiments. One month before this experiment, we tested four of the six tamarin subjects (DW, JK, SP, and UB) in a pilot experiment in which they chose between an immediate two pellets or six pellets delayed 15, 20, 25, or 30 sec. There were no statistically significant differences in indifference points for naïve or experienced subjects ($F_{1,4} = 0.28$, $p = 0.63$), although the sample size is admittedly small. Nevertheless, the two naïve tamarins showed indifference at levels within the range of the experienced individuals (Table S.1). All marmosets were naïve to the experiment to the self-control paradigm.

The subjects received their daily food allotments after the experiments were completed at the end of the day. Both tamarins and marmosets were maintained at body weights which provided the most reliable performance in food-motivated tasks.

Apparatus

We placed subjects in a metal cage (30×30×30 cm) adjacent to the discounting apparatus. There were four holes in the clear Plexiglas front panel of the cage. By reaching through the lower two holes in the wall, subjects could grasp one of two tool handles to bring the food reward within reach through the upper two holes (Figure 1). Transparent covers prevented subjects from accessing the food until the end of a delay. Two solenoids operated the movement of the covers to reveal and cover the food rewards. An experimenter flipped a

switch, starting the electronic timer and, after a specified delay, activated the solenoids to open the covers. A buzzer sounded during the delay period.

Trial procedures

A trial started with the presentation of two L-shaped tools to the subject through the lower holes in the front barrier. The tools consisted of a straight handle and a crossbar trough containing food pellets (Research Diet 45 mg banana-flavoured purified diet primate pellets). A green tool was always associated with the delivery of six pellets, whereas an orange tool always delivered two pellets. Within a session the tools remained on the same side of the apparatus, but they alternated sides between sessions. To choose one of the reward options, the subject had five seconds to touch one of the tools and 30 seconds to pull the tool until the trough contacted the front of the Plexiglas barrier of the transport cage. Minimal effort was required to pull both of the tools. Once the subjects touched one of the tools, the other was immediately removed, preventing them from switching between tools. As soon as the trough was pulled forward enough to contact the barrier, the experimenter started the delay by activating the timer. At the end of the delay, the solenoids moved the covers, allowing the subject to reach their reward. After retrieving the last pellets from the trough, the experimenter started a 30 second inter-trial interval.

Each session consisted of 14 trials and lasted approximately 15 minutes. Four of the 14 trials were forced trials; the other 10 were free choice trials. In forced trials we only presented one tool to the subject, with the other tool remaining in sight but out of reach. A session always started with two forced trials: one forced the larger reward and one forced the smaller. We alternated the order of this presentation between sessions. We randomly interspersed the remaining two forced trials (one of each choice) throughout the session. The other ten trials

were free choice trials which allowed subjects to choose between rewards by pulling one of the two tools.

Experimental design

Throughout the experiment, subjects received access to the small reward immediately (standard option). The delay for the large reward (adjusting option) was constant within a session but varied between sessions. In the first session, it started at zero and increased by one second for the next session if the subject chose the larger of the rewards seven or more times. Similarly, if the subject picked the smaller reward seven or more times, the adjusting delay decreased by one second in the following session. If the subject chose neither tool seven or more times, the delay remained the same for the next session. By adjusting the delay, we were able to find the point at which the subjects were indifferent between the smaller, immediate option and the larger, delayed option. We calculated this indifference point by comparing the mean delay to large for the last five completed sessions with the mean of the previous five sessions. Subjects reached indifference when the mean delay of the last five sessions did not differ from the mean delay of the preceding five sessions by more than 10% or one second, whichever was larger. We used the mean delay of the last five sessions as our estimate for the indifference point.

Calculating delays, handling times, and indifference points

Standard delay time (t_s) was the estimated time between toggling switch and food becoming available (0.1 sec). Handling times (h_s and h_a) were estimated from measurements of the time between the first and last reach for pellets in six forced short-delay trials and six forced long-delay trials for each subject. Each species' predicted indifference points (t_a) are a mean

of individual subject predicted indifference points. That is, we applied the rate maximization equation to each subject rather than to the overall species means. If predicted indifference points were negative for a subject, we used a time of zero sec. This accounts for the discrepancy between the stated predicted indifference point for tamarins (t_a=8.6 sec) and that calculated using the overall species means.

This experiment was conducted in compliance with the Harvard University Animal Care protocols 92-16 and 22-07.

Results

Sex differences

Although sample sizes are small, there are no sex differences in indifference point ($F_{1,7}$ = 0.06, p = 0.81) and there is no interaction between species and sex ($F_{1,7}$ = 0.01, p = 0.91).

Motivation

To further assess the role of motivation in this experiment, we examined the subjects' performance in trials within a session. We measured the proportion of choices for the larger/delayed reward (arc-sine, square-root transformed) in the last 10 sessions for each subject (the sessions used to assess the indifference point). We then divided the trials into those which occurred in the first half of the session (trials 1-5) or the second half (trials 6-10). There was a strong effect of trial ($F_{1,97}$ = 6.49, p = 0.01)—subjects chose the larger/delayed reward more in the first five trials. Significantly, there was no species effect or species by trial interaction (Figure S.1). Therefore, motivation changed within a session but was the same for both species, suggesting that their general motivational levels were roughly equal.

Table S.1: Subject data for weights, handling times, and indifference points

Subject	Species	Sex	Weight (g)	Standard handling time (sec)	Adjusted handling time (sec)	Observed indifference point (sec)
AG	Tamarin	M	413	18.3	16.5	7.6
DW	Tamarin	M	322	6.7	23.8	8.4
JG	Tamarin	F	431	11.2	21.2	9.2
JK	Tamarin	F	376	4.8	15.8	5.6
SP	Tamarin	M	435	9	39	6.7
UB	Tamarin	F	404	14.2	46	9.8
Mean	**Tamarin**		**397**	**10.7**	**27.1**	**7.9**
Ant	Marmoset	M	254	8.7	18	10
Des	Marmoset	F	340	10	21.8	16.2
Jul	Marmoset	F	394	6.2	13.8	12.8
Oth	Marmoset	M	294	8.8	20.3	13.8
Rom	Marmoset	M	335	7.7	18.5	19
Mean	**Marmoset**		**324**	**8.3**	**18.5**	**14.4**

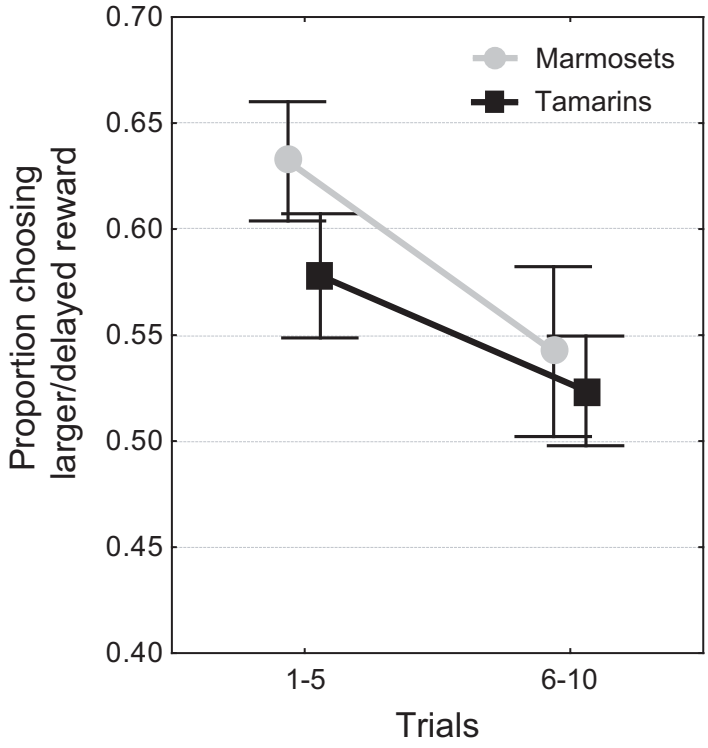

Figure S.1: Species and trial effects on choices. Both species chose the larger/delayed option more often in the first five trials of a session than in the last five trials. There is no species by trial interaction, suggesting that both species faced similar changes in motivation within a session.